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THE CYTOTAXONOMY OF THE *ASPLENIUM STUHLMANNII* COMPLEX (ASPLENIACEAE, PTERIDOPHYTA) IN AFRICA

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Key words: *Asplenium mantoniae*, *Asplenium jaundeense*, new species, chromosome numbers.

ABSTRACT

A new octoploid species, *Asplenium mantoniae*, intermediate between two tetraploids species, *A. stuhlmannii* and *A. jaundeense*, is described from West Africa. The morphology and distribution of members of the complex are consistent with the view that the octoploid has probably arisen by hybridization of the two tetraploids and chromosome duplication

INTRODUCTION

Asplenium stuhlmannii Hieron. was first described from tropical East Africa and is widely distributed from northern Tanzania to the southern Sudan. Similar, though not identical, material occurs in West Africa and was placed in *A. stuhlmannii* by Tardieu-Blot (1953) and Alston (1959) and reported by Manton (1959) to be octoploid with n = 144 chromosomes, based on meiotic analysis. Subsequent cytological examination of East African material has shown the genuine *A. stuhlmannii* to be tetraploid with n = 72 chromosomes (Appendix in Braithwaite 1964; Fig.1). Further studies of the two cytotypes suggest that they are sufficiently distinct morphologically and geographically to merit recognition as two separate species and the octoploid material from West Africa is described here as a new species, *A. mantoniae*. The new species also bears some resemblance to *A. jaundeense* Hieron., a tetraploid species (Fig.1) from West Africa, and its possible relationships to the two tetraploids is discussed.

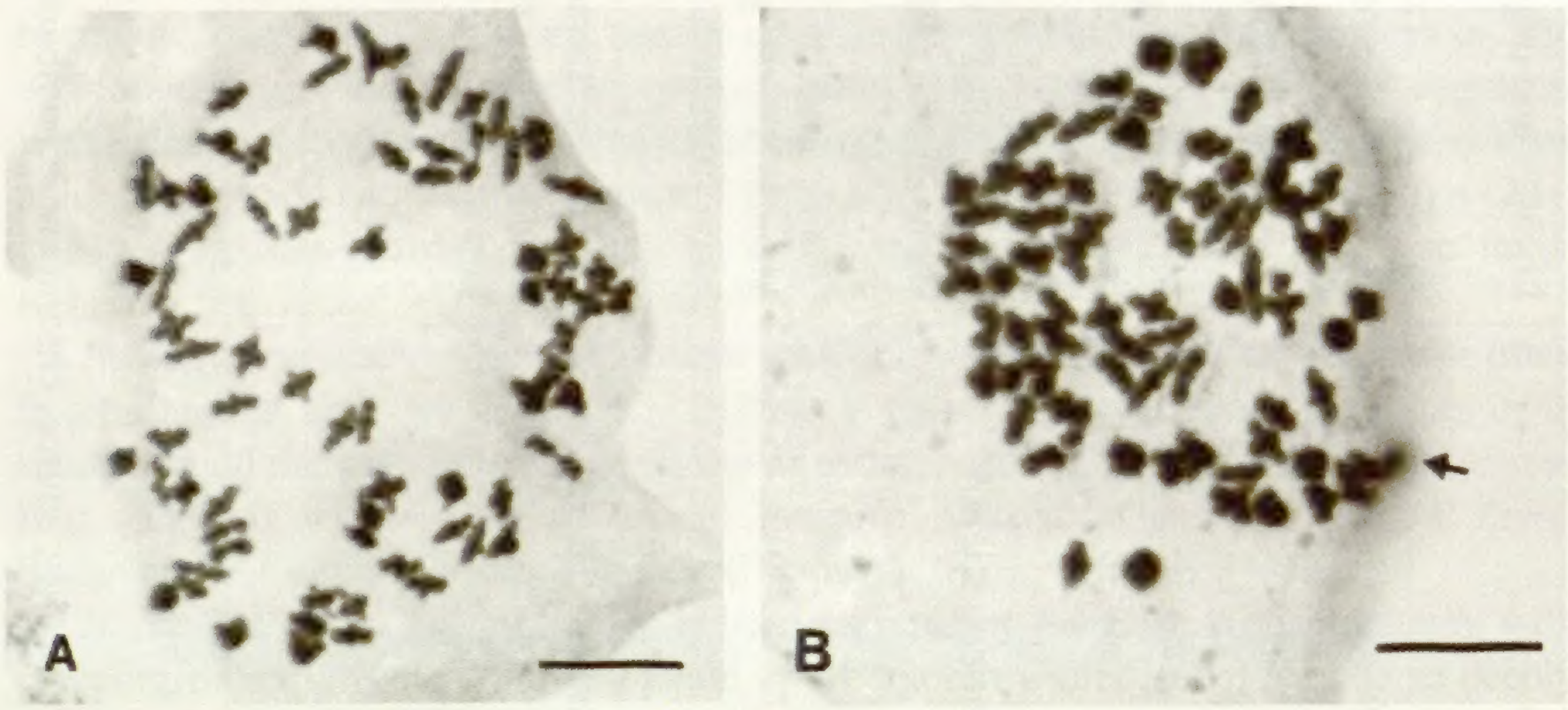

Figure 1. Acetocarmine meiotic squash preparations. A, *Asplenium stuhlmannii* n = 72, Somalia (Brittish Somaliland; B, *A. jaundeense* n = 72, arrow points to an out of focus bivalent,Yaunde, Cameroon. Scales = 10μm

Species	Locality and origin	Chromosome number	Spore size* Length	Breadth
A. stuhlmannii Hieron	Somalia, collected by Mr Desmond Kelsall (O. S Dept, St Andrews) on a hill walking expedition in 1949, ex University Botanic Gardens, St Andrews.	n = 72	40·9 ± 2·49	30·3 ± 2·06
	Kenya, living plant sent to Kew with a consignment of orchids	n = 72	39·7 ± 2·0	26·4 ± 1·0
A. mantoniae sp. nov.	Nigeria, plant raised in Leeds from spores taken from Hambler 513 (BM)	n = 144	47·1 ± 3·57	31·7 ± 2·36
	Ghana, locality not known, collected by Adams (see Manton 1959), plant in this study raised from spores taken from herb. specimen of Manton's plant	n = 144	45·7 ± 2·13	30·4 ± 2·13
A. jaundeense Hieron.	Cameroon, Yaunde, collected for the author as a living plant and first established at Kirstenbosch in 1961 then sent to Kew and subsequently transferred to Leeds	n = 72	34·1 ± 2·85	23·4 ± 1·69

* means ± SD (n = 100)

Table 1. Locality, source, chromosome numbers and spore sizes of living plants of the *Asplenium stuhlmanii* complex.

MATERIAL AND METHODS

Live plants for cytological investigation were accumulated from a variety of sources (see Table 1) and finally established in the Botanic Garden, University of Leeds. In addition, all the relevant herbarium material at BM and K was examined. Voucher specimens will be deposited in BM.

Chromosome counts were made on acetocarmine squash preparations of meiosis using the standard method for ferns (Manton 1950).

Spore samples for measurement were mounted in either gum chloral or Depex and measured using a calibrated eyepiece and ×40 objective.

THE SPECIES

***Asplenium stuhlmannii* Hieron.**

In Engl. Pflanzenw. Ost.-Afr. C: 83, 1895; type: Kassesse, Towalio in Western des Vict.-Njansa, *Stuhlman* 936 (B!—lectotype), 953!, 1179, 3246, 3981a (B—paratypes); non Tardieu-Blot, in Mem. Inst. fr. Afr. noire 28: 190, t. 36, fig. 3, 1953; Alston in The Ferns and Fern Allies of West Tropical Africa, suppl. 2 ed. Flora of West Tropical Africa, 59, 1959.

Asplenium stuhlmannii var. *laciniata* Hieron., in Engl. Pflanzen. Ost-Afr. C: 83, 1895; type: Gumango, Lande der Niamniam, *Schweinfurth* 3915 (B!—holotype; BM!, K!—isotypes).

Asplenium amoenum C. H. Wright, in Johnstone, The Uganda Prot. 1: 326, 1902, non Presl 1836; type: Uganda, E. Toro, R. Kiawiume, alt. 5000′. *Doggett* s.n. (K!—holotype).

Rhizome creeping with rather stiff loosely tufted fronds. Rhizome scales 3–5mm long, 0·5–0·75mm wide at the base, linear subulate with a rounded base and ending in a short hair point, clathrate with smooth cell walls; median cells dark thick-walled and compressed with narrow, sometimes obscured, lumens, becoming thinner walled and pellucid towards the margins. Fronds up to 24–45cm long, pinnate to deeply bipinnatifid; stipes black becoming green near apex, sparsely scaly. Lamina bright green, linear lanceolate, 15–37 × 2·5–9·5cm with 10–17 pairs of opposite or subopposite spreading pinnae. Pinnae 1·8–5·0 × 1·0–2·3cm, coriaceous, broadly trullate to trullate, base broadly cuneate; basal pinnae deeply divided, upper pinnae less so, into 3–5 lobes; largest lobes (pinnules) cuneate-obovate and further cut into 3 or 4 segments with truncate lacerate apices, smaller lobes rectangular with truncate lacerate-crenate apices. Veins and sori subflabelliform. Spores plano-convex, (32–) 36–44 (–50) × (20–) 24–30 (–35) µm perispore costate with loosely anastomosing low ridges or folds. Reproduction sexual, chromosome number n = 72 (2n = 144).

Ecology and distribution. *Asplenium stuhlmannii* is a fern of rocky outcrops often in grassland at altitudes from 850 – 2188m. It grows in sheltered rock crevices or in shade around the base of rocks or on top of rocks in the shade or less often in full sun. It is widely distributed in East Africa: Tanzania, Rwanda, Uganda, Kenya, E Zaire, Sudan and E Central African Republic (Figure 1).

Notes. The name *A. stuhlmannii* is here restricted to the East African material with creeping rhizomes bearing scales made up of smooth walled cells, pinnate to deeply bipinnatifid fronds with broadly trullate to trullate pinnae and spores with costate-alate spores with rather low smooth folds or wings (Figure 3). All the material is tetraploid in so far as can be judged from comparisons of spore measurements from specimens in

the herbaria with those from the cytologically authenticated material.

Asplenium stuhlmannii var *laciniata* with larger pinnae, more deeply dissected into laciniate lobes probably represents a larger luxuriant shade form. The rhizome scales and spore ornamentation and size match those of typical *A. stuhlmannii*.

Specimens examined. ZAIRE: Haut Zaire: Zande Dist.: entre Doruma et Niangoro, 1931, *J. Lebrun* 3180 (K, BM). SUDAN: Western Equatoria: Yambio Dist.: Mt Bangenze, in rocky crevice, in shade on hillside, local, 900m, *G. A.. Prowse* 146 (BM); *ibid.* on stone outcrop near Mt Bangenze, *F. W. Andrews* A1497 (BM); Rest House, on granite outcrop near Borago, 1939, *F. W. Andrews* A1612 (BM); Mt Ledua near Ibba, *J. G. Myers* 6570 (K); Baragu-marshes, 1939, *J. W. G. Wyld* 542 (BM). Maridi Dist..: Azza Forest, in crevice of rocks in depression forest, tufted frond, local, 850m, 1953, *Prowse* 153 (BM); near Azza Forest, 1939, *F. W. Andrews* A1347 (BM). Eastern Equatoria: Yei Dist.: Lado, Yei R., *F. Sillitoe* 110 (K); Kapigo, in pockets of earth on open rocky hillside especially near bushes, common, 1273m, 1953, G. A. *Prowse* 33 (BM); Mt Gumbiri, in Selaginella mats on open rock surface, common, 1500m, 1953, G. A. Prowse 17 (BM); Mt Kala, rocky crevice and under *Euphorbia* sp., locally common, 1200m, 1953, *G. A. Prowse* 191 (BM); Imatong Mts, Talanga, 4° 01′ N, 32° 45′ E, 950m, 1980, *I. Friis & K. Vollesen* 577, 578 (K). UGANDA: Northern Prov.: West Nile Dist.: Koboko Hill, damp crevices in granite rocks, 4400ft, *R. J. Chancellor* 111 (K); Mt Otzi,, 500ft below summit, 5000 feet, fairly common, 1951, *E. M. Cherry* 5 (K, BM). Acholi Dist.: Chua, fern on rocky outcrop at Ukuti, 1935, *W. J. Eggeling* 2411, 2413 (K); Lotuturu, Chua, *Maxwell-Forbes* 94 (PRE). Lango Dist.: Maruzi, ground fern growing in interstices of rocks of Kibuji Hill, 1937, *R. G. Sangster* 321 (BM). Buganda Prov.: Mubende Dist., Bugangadzi, grows on granitic rocks, 4200ft, *Dawe* 137 (K). Mengo Dist., Entebbe, Loe, 1909, *R. Fyffe* 71 (K). Western Prov.: Toro Dist.: Kyaka, growing on tree trunk, 4500ft, 1913, *J. D. Snowden* 150 (K), 1914 (BM); Mwenge, Oruha Hill, fern in crack of gneiss rock, 1951, *H. A. Osmaston* 1221 (BM); Kyegegwa, granitic outcrop, 4200ft, 1933, *A. S. Thomas* (K). Ankole Dist.: Igara, rocky outcrop in

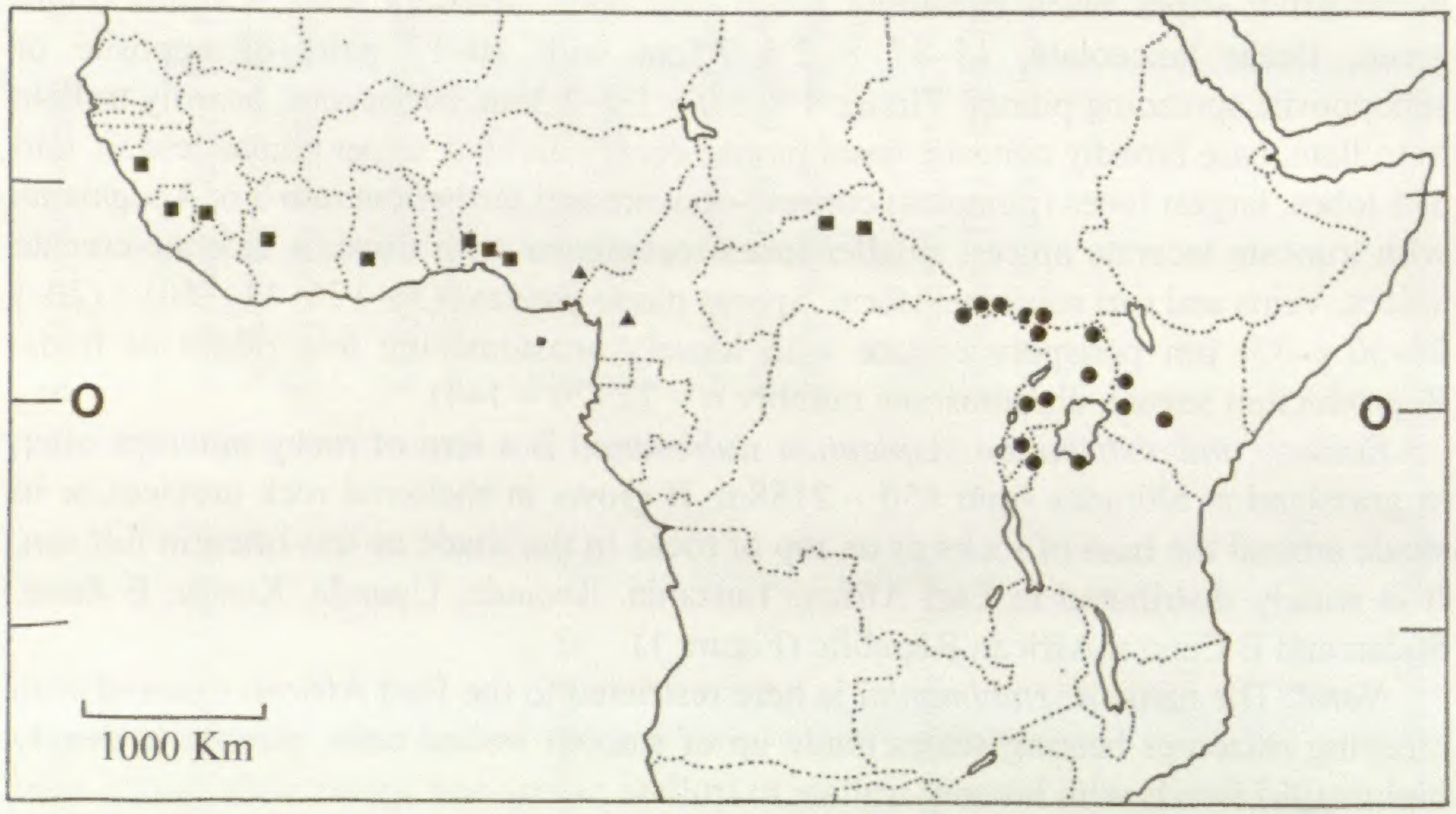

Figure 2. Distributions of *Asplenium stuhlmannii* (●), *A. jaundeense* (■) and *A. mantoniae* (▲). The locality of *A. jaundeense* in Gabon not placed.

short grassland, 5500ft, 1939, *Purseglove* 577 (K); Nyakalakye-Buyenja, Kashari, 0° 22′ S, 30° 31′ E, growing in and around rock crevices, 1680m, 1986, *P. K. Rwaburindove* 2235 (K). Eastern Prov.: Teso Dist.: Kyere, crevices among rocks forming rocky outcrops, 3650ft, *P. Chandler* 971 (K). Busoga Dist..: Bulimba Banga, hill N of Mpumuda, Kibili Rd, growing in shade under large round boulders on hill top, 1950, *G. A. T. Wood* Y2 (K). KENYA: Rift Valley Prov.: Trans-Nzoia Dist.: NE Elgon foothills, Simpsons rocks, rock crevice in outcrop rock in savannah, 6200ft, *Tweedie* 1832 (K). Eldoret Dist.: Oldan Sapuk, *c.* 7000ft, 1951, *P. J. Greenway* 8538 (BM). Yanza Prov.: North Kavirondo Dist.: S foothills of Elgon above Kimilili, growing in rock crevices, 5900′, *Tweedie* 2921 (K). Uasin-Gishu Dist.: Oldan Sapuk, c. 7000ft, 1951, *P. J. Greenway* 8538 (K). Nandi Dist.: Kaimosi Farm, 5800ft, *G. R. Williams* 571 (K). Central Prov.: Fort Hall Dist..: Fort Hall, 1903, *R. Meinertzhagen* s.n. (BM). Coastal Prov.: Teita Dist..: Teita Hills, Mwatata R. Valley 5.8km Mwatata-Wundanye along new alignment, 870–1000m, *R. B. Faden* 70/443 (K). ? Masai Prov.: Masai Dist..: Emoli Hill ft, 5900ft, *Opiko* 326 (K). TANZANIA: Lake Prov.: Mwanza Dist.: coast of Speke Gulf near Mwanza, moist cracks and hollows below great granite boulders, 3740ft, 1931, *B. D. Burtt* 2474 (K, BM); Mwanga, fern common on rocky hills near Lake Mwanga, 19385 (?8), *P. E. Glover* 303 (K). Ngara Dist.: Bugarama, Bushubi, on rock face in crevice, 5000ft, 1961, *R. Tanner* 5829 (K). RWANDA: Biumba Territory, Region de Mutara, env. de Mimuli, colline Nyakagenge, anfractuosités dans affleurements granitiques, 1975, *Troupin* 3726 (K); *ibid.*, creux ombragé sous roche surplomb, 1975, *Troupin* 3267; *ibid.*, affleurements rocheux, 1450 – 1500m, 1975, *Troupin* 4212 (K).

Asplenium mantoniae A. Braithw. sp. nov.

Asplenium stuhlmannii et *A. jaundeense* similis sed differt chromosomate numero (n = 144) et sporis majoribus; a *A. stuhlmannii* pinnis trapezio-trullatis, basaleis acutis et lobis paucioribus; a *A. jaundeense* lobatis profunde trapezioid-trullatis pinnis.

Holotypus: Nigeria, Ondo Province, insel-berg nr Ado Aiye, 7° 54′ N, 3° 30′ E, with creeping rhizome growing under overhanging boulders, *Hambler* 513 (BM).

Asplenium stuhlmannii sensu Tardieu-Blot, in Mem. Inst. fr. Afr. noire 28: 190, t. 36, fig. 3, 1953; Alston in The Ferns and Fern Allies of West Tropical Africa, suppl. 2nd ed., Fl. W. Trop. Afr., 59, 1959.

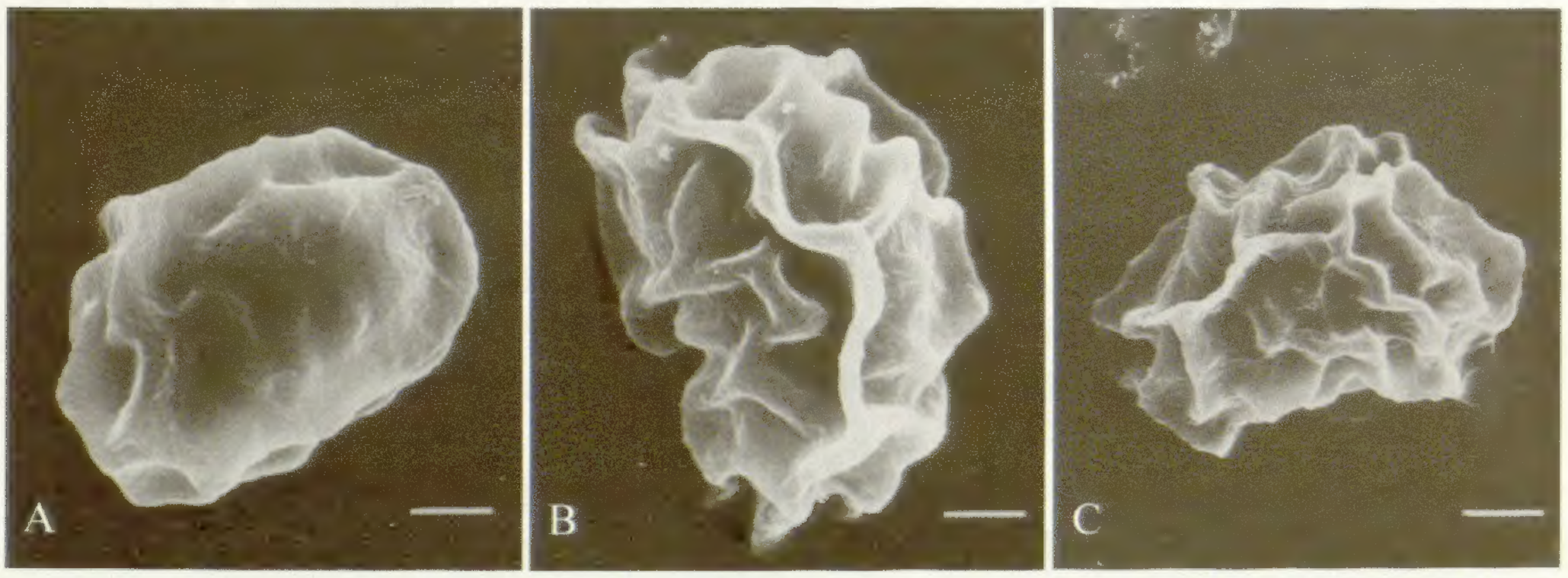

Figure 3. Morphology of the *Asplenium stuhlmannii* complex, spores. A, *A stuhlmannii*, Somalia; B, *A. mantoniae*, Hambler 513; C, *A. jaundeense*, Yaunde, Cameroon. Scales: A – C = 10 μm.

Rhizome creeping with stiff tufted fronds; rhizome scales dark brown, up to 6mm long, 1mm wide, linear-subulate, clathrate, cell walls thick and opaque in the middle, becoming thinner and pellucid towards the margin, walls facing lumens often irregularly minutely denticulate (Figure 3). Fronds 15–44cm long, pinnate to deeply pinnatifid; stipe dark purplish brown 4·5–20cm long with small scales similar to those of the rhizome at the base; rachis dark purplish brown, for the most part becoming green towards the apex, sparsely scaly. Lamina 10–24cm long, 3·5–7·5cm wide, narrowly ovate with 8–13 pairs of subopposite spreading pinnae merging into a lobed apex. Pinnae 2·0–6·5 × 0·75–2·5cm, narrowly parallelogram-shaped to trapezoid-trullate, base narrowly cuneate then divided into 3–4 lobes merging into lacerate-serrate, sometimes attenuate, acute apex (Figure 2); largest basal acroscopic lobe obtriangular to rectangular and further cut into 3 lobes with irregularly crenate apices, remaining lobes rectangular with irregularly crenate apices, becoming progressively smaller towards apex of pinna. Veins and sori subflabellate. Spores plano-convex, (40–) 46 – 48 (–55) µm × (28–) 31–32 (–37) µm, costate-alate with much anastomosing high wavy (undulating) ridges or wings. Reproduction sexual, chromosome number n = 144 (2n = 288).

Ecology and distribution. This new species is generally associated with rocky outcrops, usually but not exclusively granite, e.g. the inselbergs of Nigeria, where it is found in the shade on rock faces, in damp rock crevices or growing under overhanging boulders from 100 – 400m. It has a predominantly West Africa distribution (Guinea, Sierra Leone, Ivory Coast, Ghana, Nigeria, Cameroon) with outliers in the Central African Republic (Figure 2).

Notes. The new species resembles *A. stuhlmannii* in its general growth habit, frond architecture, colour and texture, but is distinguished by its slightly larger rhizome scales made up of cells with thicker and often dentate cell walls, generally larger but less divided and more trapezioid or parallelogram-shaped pinnae with narrower cuneate bases and by its larger costate-alate spores with broader more frequently anastomosing wavy (undulating) perispore folds or wings. In these respects it resembles the following species, *A. jaundeense*, despite being traditionally confused with *A. stuhlmannii.* (see Figures 2 & 3).

Etymology. Dedicated to the late Professor Irene Manton F. R. S. in recognition of her contribution to knowledge of the cytology of the fern flora of West Tropical Africa. specimens examined. GUINEA: Haut Niger (Fouta Djallon): Mt Bambaya, vers 100m, 1945, *P. Jaeger* 2113 (K); Macenta, *Adams* 5513 (P); Gueckedou, *Adams* 5581 (P). SIERRA LEONE: Northern Prov., Bumba (?Bumban), 1200ft,1932, *R. Glanville* 436 (BM). IVORY COAST: Séguéla, rocher granitique a 15km E. sur la route de Beoul, sous un surplombe humide, 1948, *H. des Abbayes* 619 (BM); entre Seguela et Maukono, fissure rocheuse, 1954, *R. Schell* (K); Rocher d'Issia, in groove on granitic rock, 250m, 1962, *A. J. M. Leeuwenberg* 4140 (K); Pays des Ayoles, sommet du Mont Kouan prés Aanamé (manelog granitique), 400m, 1909, *A. Chevalier* 21269 (K,P); Mt Dou, Man, *Porteres* s.n. (P); Mt Semelebou, *A. Chevalier* 22095 (P). GHANA: Bhongo-Ahafo Prov.: Ebaw Rock near Mim, growing in moist crevices on granite outcrop near thicket margin, 1973, *Hall & Abbiw* 44559 (K). NIGERIA: Oyo Prov.: hill 3 km N of Iseyin, 7° 58′ N, 3° 34′ E, 350m, rather shady crevice in granitic rocks, 196?, *J. B. Gillett* 15399 (K); Okeho, group of low hills about 3 miles from Iseyin road, in savannah country, 1959, *R. W. J. Keay* FHI 37748 (K); Ibadan, Oje Rock, sheltered rock crevices near summit, 1967, *D. P. M. Guile* 3018 (K). Ondo Prov.: Erio near Aramoko-

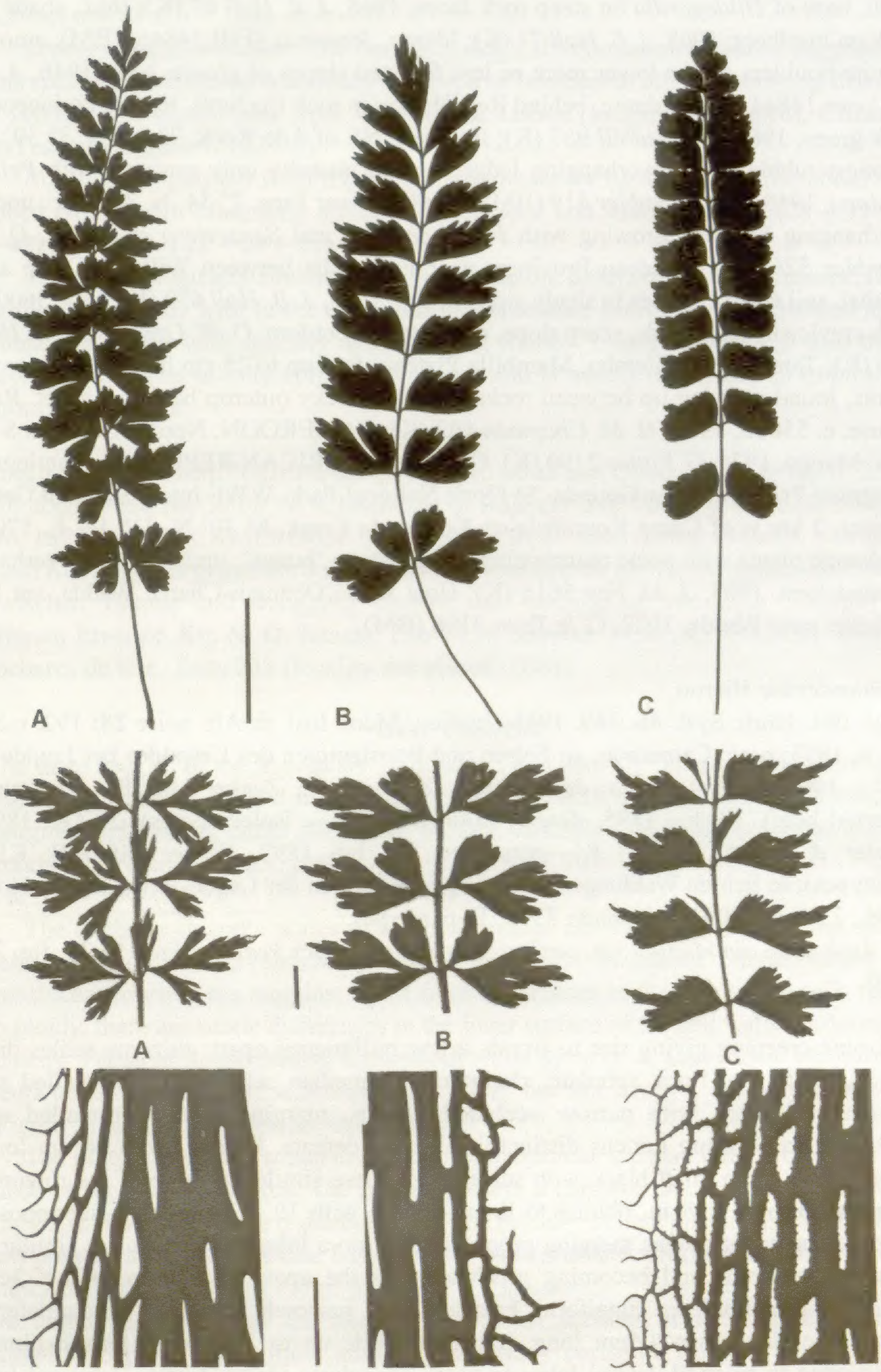

Figure 3. Morphology of the *Asplenium stuhlmannii* complex showing silhouettes of fresh juvenile fronds (top, scale = 5cm), pinnae from lower part of mature dried fronds (middle, scale = 2 cm) and sections (middle to margin, scale = 0·1mm) of the rhizome scales (bottom). A, *A. stuhlmannii*, Somalia; B, *A. mantoniae*, Hambler 513; C, *A. jaundeense*, Yaunde, Cameroon.

Ekiti, base of *Hildegardia* on steep rock faces, 1968, *J. B. Hall* 67 (K); *ibid.*, shade of rock on inselberg, 1968, *J. B. Hall* 71 (K); Idanre, *Jones* s.n. (FHI 14846) (BM); among granite boulders on the lower more or less forested slopes of granite hills, 1946, *A. P. D. Jones* 14844 (BM); Idanre, behind Rest House, in rock fractures, texture coriaceous, dark green, 1968, *D. Gledhill* 957 (K); inselberg NE of Ado Rock, 7° 51′ N, 3° 30′ E, amongst rubble under overhanging ledge – small quantity only growing with *Pellia doniana*, 1958, *D. J. Hambler* 419 (BM); inselberg near Tapa, 7° 34′ N, 3° 30′ E, under overhanging boulders growing with *Pellia doniana* and *Sanseviera* sp., 1958, *D. J. Hambler* 526 (BM). Plateau Province: near Farm Rua between Willsani Camp and Marhai, soil filled crevices in shady side of rock, 1968, *J. B. Hall* 659 (K); Sha, 3600ft, rock crevice in deep shade, scarp slope, dark green erect fern, *D. W. Lawlor & J. B. Hall* 570 (K). Taraba Prov.: Gembu, Mambilla Plateau, fern up to 25 cm high with grooved rachis, found growing up between rocks on a wet rocky outcrop behind the Vet. Rest House, c. 5500ft, 1973, *H. M. Chapman* 102 (K). CAMEROON: Nord Prov.: 7km S of Poli, Mango, 1974, *G. Fotius* 2190 (K). CENTRAL AFRICAN REPUBLIC: Bamingui-Bangoran Prov., Manova-Gounda- St Floris National Park, WWF Inter. Elephant Cons. Project, 2 km w of Camp Koumbala on Koumbala Creek, 8° 30′ N, 21° 12′ E, 570m sandstone plants with some outcropping of sandstone 'buttes', under shaded overhang in sandstone, 1983, *J. M. Fay* 5615 (K). Haut Kotto(Obangui-Chari): Wadda, sur les rocheurs near Wadda, 1922, *G. le Testu* 4106 (BM).

A. jaundeense Hieron.
Engl. Bot. Jahrb. Syst. 46: 369, 1911; Tardieu. Mem. Inst. fr. Afr. noire **28:** 192, t. 36, fig. 4, 1953; type: Cameroon, an Felsen und Baustammen des Urwaldes bei Jaunde in 800 – 1000 Hohe ü. M., in dem Jahren 1890 – 1892, *Zenker* 214 (B!—lectotype, selected here), 1894 – 1895, *Zenker* 214a (K!, BM!— isolectotypes); 23 Okt 1894, *Zenker & Staudt* 526 (B! K!—paratypes); 31 Juli 1897, *Zenker* 1492 (B, K!—paratypes); in lichten Waldungen an steinigen abhangen der Lagoo-Berge in 300 Hohe ü. M., 25 Juni 1909, *Ledermann* 4396 (B–paratype).

Asplenium dimidiatum var. *zenkeri* Hieron., in Engler *Veg. der Erde* **9:** 28, fig. 24, 1908.

Rhizome creeping giving rise to fronds a few millimetres apart; rhizome scales dark brown, up to 6 × 1mm, subulate, clathrate with median cells dark thick-walled and compressed, often with narrow occluded lumens, marginal cells thin-walled and pellucid, walls facing lumens distinctly minutely dentate. Fronds up to 66 cm long; stipes up to 26cm, matt black with scales at the base similar to those of the rhizome. Lamina up to 41 × 8cm, oblong to linear-oblong with 10 – 20 opposite-subopposite pairs of spreading pinnae merging progressively into a lobed apex; rachises similar to stipe but glabrous and becoming green towards the apex. Pinnae up to 6 × 3cm, trapezoid-rhomboid to cuneiform hastate, base narrowly cuneate, inaequilateral, acroscopic side up to 1·5cm long, basiscopic side up to 3cm long; largest pinnae subtrilobed to trilobed, lateral lobes truncate irregularly inciso-dentate, terminal lobe long, elongate-deltoid, sparsely alternately inciso-dentate, ending in an acute point; trilobing tending to disappear and pinnae becoming trapezoid-rhomboid towards apex and in juvenile fronds. Costae not evident, veins and sori subflabellate. Spores plano-convex, (28–) 33–36 (–40) µm × (19–) 22–24 (–27) µm, perispore costate-alate with anastomosing high wavy ridges or folds (wings). Reproduction sexual, chromosome

number n = 72 (2n = 144).

Ecology and distribution. The limited ecological information available suggests that this species is associated with rocky outcrops or boulders at altitudes ranging from 300 – 1000m. It is known only from West Africa: Gabon (locality not placed), Cameroon and eastern Nigeria (Figure 2).

Notes. Distinguished from *Asplenium mantoniae* by its trapezioid- rhomboid three lobed pinnae with often long attenuate apical lobe and smaller spores, (28–) 33 – 36 (–40) µm × (19–) 22 – 24 (–27) µm.

The morphologically similar *A. megalura* Hieron. differs by its erect rhizome, rather brittle wiry fronds with fewer and often long-attenuate pinnae, a large 3-lobed apical pinna and spores with sparsely anastomosing shallow ridges or wings. It also differs ecologically being usually epiphytic in forest and is widely distributed in tropical and subtropical Africa.

Specimens examined. NIGERIA: Ogoja Prov.: Ikom and Obudu Divs, nr top of 2500ft hill about pillar no. 30 on the E boundary of Boje enclave, *Jones & Onochie* s.n. (FHI No. 18757) (BM). CAMEROON: Milbraed, III Reise nach Afrika 1913-14. Ubergangs –und Kampfgebiet gegen die Savanna an der Nord-grenze der Hylea südlich des Sanaga zwischen Yaunde und Dangdeng umwelt der Vereinigung von Lom (Sanaga) und Djerem Etwa 68 Km N. O. Jaunde, Feb 1914, *Sommer* 8718 (K). GABON: Andoun, rocheres de tete, *Testu* 238 (locality not placed) (BM).

DISCUSSION

The three species of the *Asplenium stuhlmannii* complex are united by the presence of a creeping rhizome clothed in clathrate scales with dark median band and translucent margins, and bearing rather stiff once- pinnate narrowly lanceolate or narrowly ovate fronds. The rhizome scales, pinnae and spores of the three species are shown in Figures 2 & 3.

The clathrate rhizome scales of all three species are made up of dark thick-walled cells with compressed lumens in the middle parts becoming thinner-walled and translucent towards the margins. Apart from differences in the size of the cells related to ploidy, there are subtle differences in the inner surface of the cell walls bordering the lumens. Those of *A. stuhlmanni* are smooth while those of *A. jaundeense* are minutely denticulate. Those of *A. mantoniae* are often, but not always, sparsely denticulate (Figure 2), and thus somewhat intermediate.

The pinnae and spore ornamentation of *A. mantoniae* are also intermediate between those of the two tetraploids. The pinnae possess a narrower acute base and are more trapezoid-rhomboid and less dissected than the broadly trullate pinnae of *A. stuhlmannii* and possess a broader cuneate base and are more trulllate with deeper lobes than the trapezio-rhomboid almost entire pinnae of *A. jaundeense*. The spores of *A. mantoniae* are larger than those of the two tetraploids on account of their higher level of polyploidy. Their higher more anastomosing wavy perispore folds or wings contrast with the rather low sparingly anastomosing straight perispore wings of *A. stuhlmannii*. In this respect they resemble the spores of *A. jaundeense*.

The morphological analysis suggests a close relationship between the three members of the complex and is consistent with the view that *A. mantoniae* has most likely arisen by hybridisation between the two tetraploids and subsequent doubling of the chromosome number of the hybrid to produce the octoploid. The present

distributions of *A. jaundeense* and *A. stuhlmannii* are widely separated in West and East Africa respectively so that such a hypothesis would imply that in the past their distributions must have either been sympatric or in close contact. The distribution of *A. mantoniae* partly falls between those of the two tetraploids, but has also extended the distribution of the complex particularly in West Africa where it may now be found as far west as Sierra Leone and Guinea.

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ASPLENIUM DELAVAYI (PTERIDOPHYTA, ASPLENIACEAE) A FERN SPECIES NEW TO NEPAL

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Key words: *Asplenium delavayi*, Pteridophyta, west Nepal, disjunct

ABSTRACT

Asplenium delavayi (Franch.) Copel., a Sino-Himalayan species, described from S.W. China and previously known only as far west as Sikkim, has been discovered in the Baitadi District of west Nepal. This is much further west than might be expected and emphasises the possibility of more species being discovered in Nepal with increased collection and study.

INTRODUCTION

Although Nepal is only *c.* 885 km from west to east and 145 to 241 km from north to south, it contains extreme differences in climatic and geographic situation, as a result of the great range of altitude, from *c.* 60 m. in the southern *terai* zone to more than 8000 m. in the high Himalaya. Plant diversity ranges from stunted alpines surviving in harsh environments in the frozen mountains, to mighty trees of the steamy lowland jungles. This diverse environment provides habitats for a surprisingly large number of plant species and more than 6000 species of flowering plants have been recorded so far from Nepal. It has been estimated that over 6600 species will be listed from the country when the poorly known remote regions are fully explored (RBGE 2007).

Nepal also has a rich fern-flora with 532 species of pteridophytes reported so far (Thapa 2002; Fraser-Jenkins & Thapa in prep.). Nepalese pteridophytes belong to two main phytogeographical elements, with a smaller third element. The dominant group of species are Sino-Himalayan species, with their centre of diversity in S.W. China, which have spread westwards along the Himalayan chain and are typically plants of the main and inner ranges, occurring from mid to higher altitudes, though some may occur in the lower, outer ranges nearer the plains. Such species usually occur more-or-less throughout Nepal, though the number of species is higher in the higher rainfall areas of the east. The second group of species are the S.E. Asian elements, which require more tropical conditions and high rainfall. They occur predominantly in E. Nepal from lower-mid to mid altitudes, and although they also extend westwards through Nepal, their numbers decrease rapidly further westward, particularly towards far-west Nepal. There is a small second enclave of S.E. Asian species in the locally high-rainfall area around Pokhara in W.C. Nepal. The third element is a small group of either European or W. Himalayan species, the latter a special part of the Sino-Himalayan group. These extend eastwards from the W. Indo-Himalaya into the far-west part of Nepal, with several occurring mainly behind the Himalayan line in C. Nepal.

Asplenium is one of the larger genera in the flora and contains 32-34 species and an additional subspecies in Nepal (Thapa 2002, Fraser-Jenkins & Thapa in prep.) of which 19-21 species may be considered Sino-Himalayan elements, eight S.E. Asian elements and five European elements (Fraser-Jenkins pers. comm., Dec. 2007). Most new

records for Nepal concern what is presumably the richest part of the flora in eastern Nepal. But the central region is by far the best collected due to its greater accessibility and, as currently known, more species are recorded from central Nepal than further east. This is likely to be an artificial anomaly resulting from the greater attentions of collectors there. The least known area is western Nepal, especially the far west. There is a higher proportion of semi-arid and European and W. Himalayan elements here, but it is clear that fewer species occur in W. Nepal due to the lower rainfall. However because the area is so under-collected some surprises occasionally turn up there, with some species extending further west than might be expected.

In 1997, the author came across an unusual species in far W. Nepal which was not familiar to him. It had the long, indusiate sori of an *Asplenium*, but a uniquely rounded, entire and simple lamina of small size, and a black stipe. This was subsequently identified in Dec. 2007 by C.R. Fraser-Jenkins as the very rare and little known species, *Asplenium delavayi* (Franch.) Copel., which was not previously known from Nepal, even in the east.

TAXONOMIC TREATMENT

Asplenium delavayi (Franch.) Copel., *Genera Filicum*: 165 (1947).

Basionym: *Scolopendrium delavayi* Franch., *Bull. Soc. Bot. France*, sér. 2, 32: 28 (1885); synonyms: *Phyllitis delavayi* (Franch.) C.Chr., *Index Fil.* 2: 492 (1906); *Schaffneria delavayi* (Franch.) Tardieu, *Naturaliste Malgache* 9(1): 30 (1957); *Sinephropteris delavayi* (Franch.) Mickel, *Brittonia* 28(3): 327 (1976).

Type: China, Yunnan: "in montibus, ad Chouang-che-teou, supra Ta-pin-tze, prope Tali [now Dali]". *Abbé P.J.M. Delavay* 67, 19 Aug. 1883 (P, K).

Distribution: W. Nepal, Sikkim, Bhutan, N.E. India (Manipur), N. Myanmar, S.W. and S.C. China (Yunnan, Sichuan, Guizhou and Guangxi).

Asplenium delavayi was illustrated by Clarke (1888), who first reported it from India, Ching (1930), Mickel (1976) and Wu (1999) and is probably related to the similar, but larger, Chinese and Japanese species, *A. cardiophyllum* (Hance) Baker (syn.: *Boniniella cardiophylla* (Baker) Tagawa). Although several splinter-genera, including *Sinephropteris*, were raised at various times, these are now generally sunk

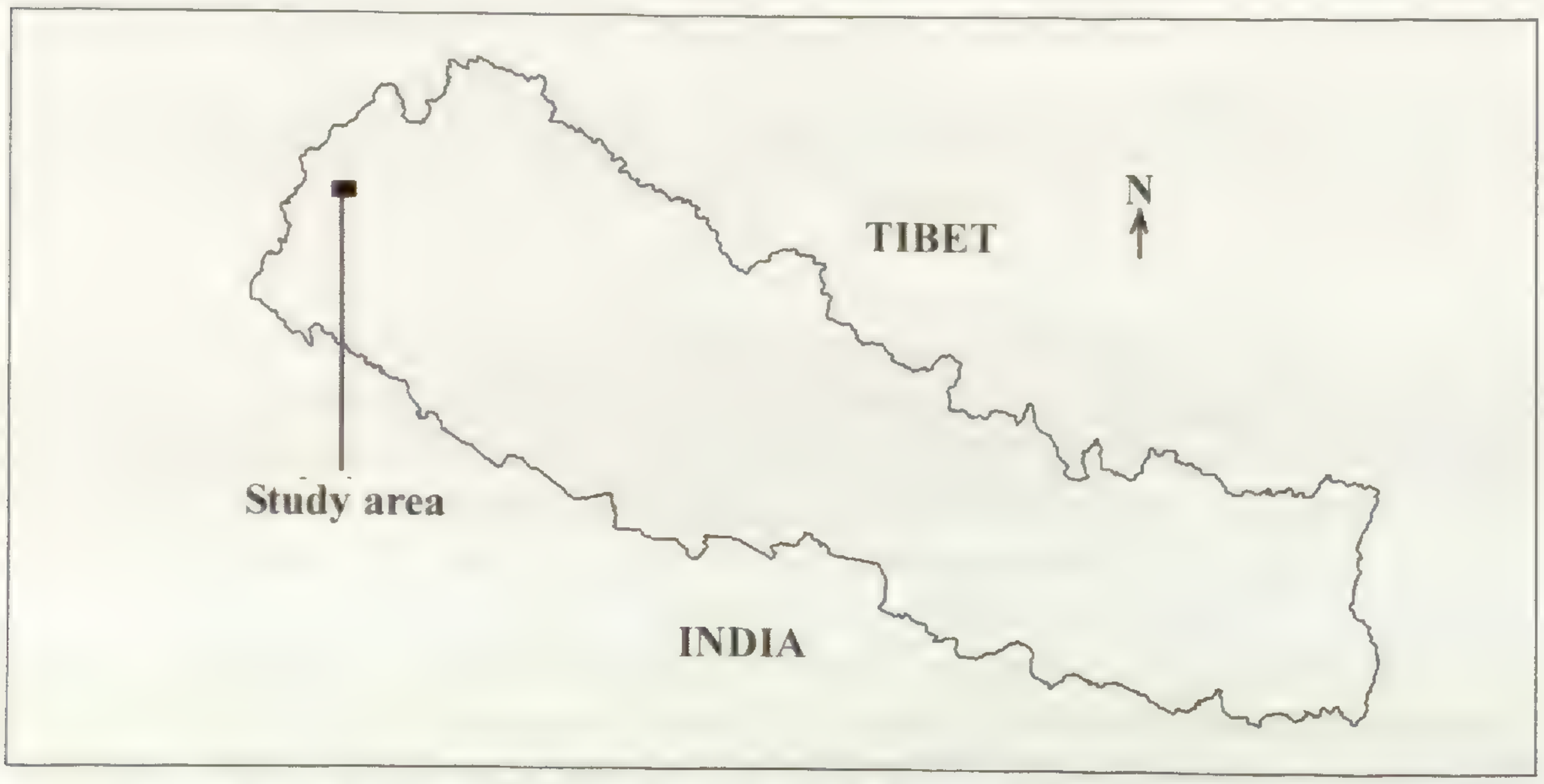

Figure 1: Map of Nepal showing the location of *A. delavayi* in Baitadi District.

into *Asplenium* as they all have a recognisably similar "asplenioid" morphology and are connected by intermediate species to the main-stream of the genus.

Asplenium delavayi was collected by the author in Nepal at Nwaghargad, Baitadi District, Far-West Development Region (Mahakali Zone); in crevices of damp rock in open places, 1258 m. alt. (4125 ft.). *A. Rijal* 3251, 15 January 1997 (KATH). The distribution of *A. delavayi* is that of a Sino-Himalayan species, though occurring at lower altitude.

Description: *Rhizome* short, unbranched, up to *c.* 1cm. long, erect, bearing a tuft of branched, dark-brown roots below, scales on the apex similar to those on the stipes but slightly smaller, and a tuft of semi-erect, radiating stipes. *Stipes* cylindrical with an adaxial groove, blackish-brown to black, glossy, 2.5-5cm. long, erect, bearing a tuft of small, greyish, narrowly lanceolate, acuminate, slightly toothed scales towards their bases, *c.* 2-3mm. long, 0.4-0.7mm. wide towards their bases. *Lamina* persistent in Winter, simple, 2-2.6 x 2.1-2.6 cm., glabrous above, bearing a few scattered small scales beneath, bright green, paler below, entire to slightly wavy at the margin, markedly rounded-ovate with a shallow cordate base and sometimes a slightly rounded-pointed apex, a vague darkish midrib present towards the base of the lamina, veins immersed, inconspicuous, radiating from the midrib, several times dichotomously forked, with the smallest forks towards the margin, but not reaching it, with occasional anastomoses near to the margin. *Sori c.* 20-28 per frond, elongated, straight to slightly curved, placed along the veins, not forked, obliquely radiating, starting near the midrib and ending below the margin, larger main sori *c.* 1cm. long, occasional smaller sori borne between the larger sori from about half way along their length, indusiate; *indusium* pale, very thin, becoming brown, lifting and shrivelling somewhat on soral ripening, opening towards the adaxial (midrib) side, Spores good, regular, bilateral, with short wings of perispore, *c.* 28 x 20 µm.

The general habit of the fern is similar to a small, more delicate *Adiantum reniforme* L. (from Macaronesia and S.W.China), but with the lamina not horizontal as in that species and the sori elongated and radiating on the lower surface of the frond, not short and around the edge. It is also similar to a very small *Asplenium scolopendrium* L. (from N. America, Europe, Macaronesia, W. Asia, China and Japan), but with round, not elongated ovate fronds and thin, black stipes.

CONCLUSION

The discovery of this rare species in far-west Nepal where it has been overlooked so far is probably connected with that area being under-collected. The considerable disjunction of this population from those further east is not likely to be an actual botanical reality. It is also likely that further unrecorded species may be found if more intensive collecting were made, particularly if carried out by specialists familiar with all the Nepalese pteridophytes who could easily pick out any unfamiliar taxa. Some other species also show similar disjunctions which may be expected to be only temporary until further study has been made. At one time there was a considerable gap in recording between Darjeeling/Sikkim and the W. Himalaya in Kumaon (Uttarakhand) for the majority of species extending that far west. But since the pteridophyte-flora of Nepal has become largely known over the latter half of the 20th Century, to date, the "central Himalayan gap" has largely been filled and can be seen as an artificial one. A few large disjunctions still remain, these are:

Acrophorus paleolulatus Pic.Serm. - gap from C. Nepal to Kumaon (Chamoli).

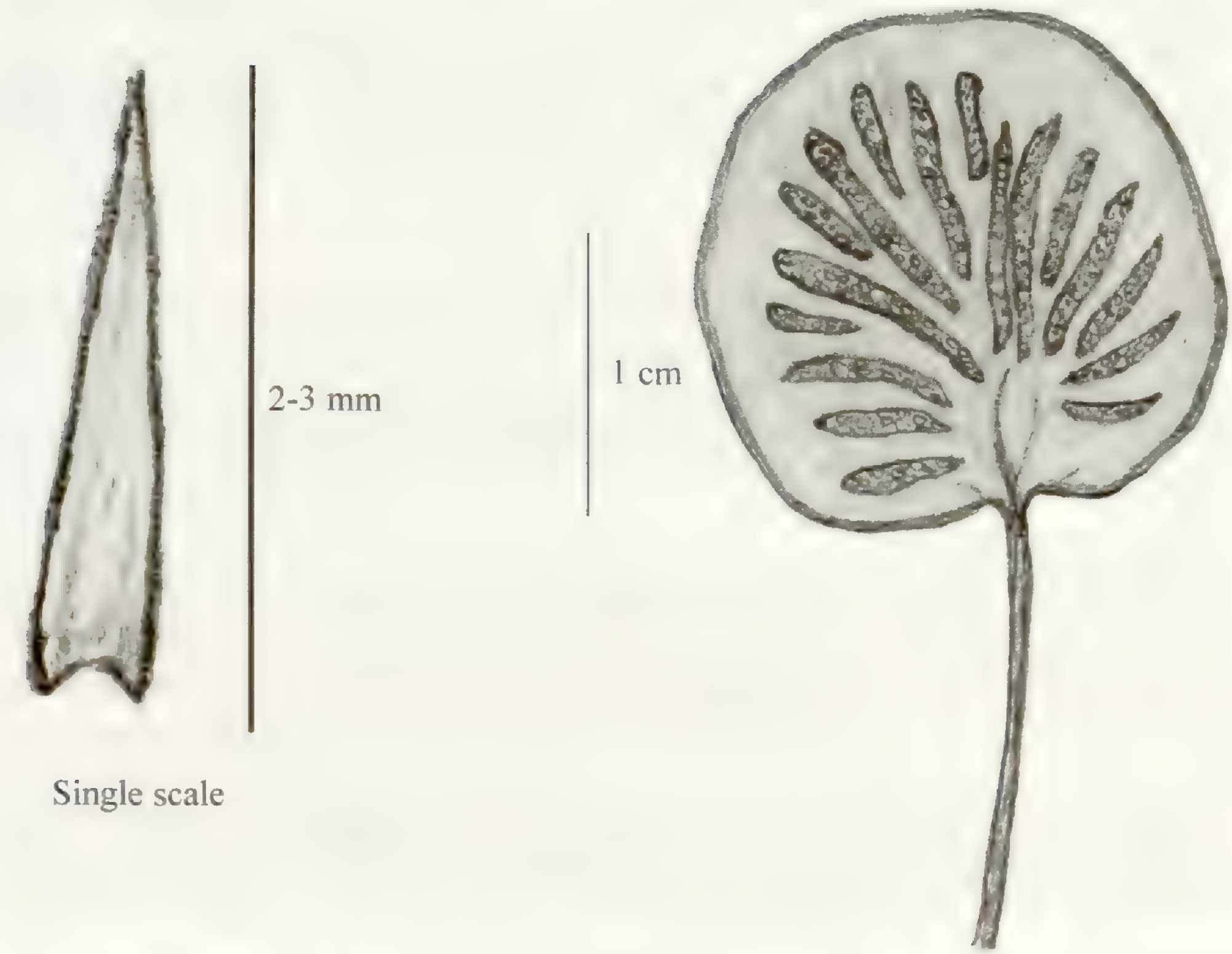

Figure 2: Sketch of the general habit, a stipe-base scale and the abaxial surface of the frond with sori.

Actiniopteris radiata (Sw.) Link - gap from E. Nepal to Lumaon (Garhwal).
Acystopteris tenuisecta (Blume) Tagawa - gap from E. Nepal to Kumaon (Nainital).
Anogramma reichsteinii Fras.-Jenk. - gap from C. Nepal (Chapagaon, Kathmandu; locality perhaps doubtful) to Kumaon (Nainital).
Asplenium delavayi (Franch.) Copel. - gap from Sikkim to far-west Nepal (Baitadi).
Athyrium otophorum (Miq.) Koidz. - gap from N.E. India (Meghalaya) to Kumaon (Pithoragarh).
Athyrium roseum Christ - China; Darjeeling (*Fraser-Jenkins*) and gap to W.C. Nepal (below Annapurna Base-Camp. *Fraser-Jenkins*).
Cornopteris quadripinnatifida M.Kato - gap from C. Nepal to Kumaon (Chamoli).
Deparia lancea (Thunb.) Fras.-Jenk. - gap from C. Nepal (Sankhu) to ?Kumaon (Pithoragarh. *Punetha & Kholia*).

Plate 1 & 2: *Asplenium delavayi* from Baitadi, general view.

Dryopteris pulvinulifera (Bedd.) Kuntze - gap from E. Nepal to Kumaon (Nainital).
Lepisorus sublinearis (Baker *ex* Takeda) Ching - gap from W.C. Nepal (Pokhara) to Kumaon (Nainital).
Lindsaea commixta Tagawa - gap from N.E. India (Assam) to W.C. Nepal (Andheri Khola, N. of Tansen; locality sometimes given on label as Mussoorie in error).
Matteuccia intermedia C.Chr. - gap from W.C. Nepal (Annapurna Base Camp. *Fraser-Jenkins*) to Kumaon (Pithoragarh).
Microlepia hallbergii (d'Almeida) C.Chr. - gap from C. Nepal (Sankhu) to Kumaon (Garhwal).
Microsorum zippelii (Blume) Ching - gap from far E. Nepal to Kumaon (Chamoli).
Pteris kathmanduensis Fras.-Jenk., in prep. - gap from C. Nepal (Kathmandu) to Kumaon (Pithoragarh).
Pteris vittata L. *subsp. vermae* Fras.-Jenk. - gap from China, Tibet and ?Bhutan (Thimphu. *Fraser-Jenkins*) to Kumaon (Nainital).
Thelypteris (*Christella*) *lebeufii* (Baker) Panigrahi - gap from N.E. India (Assam State) to Kumaon (Tanakpur. *Fraser-Jenkins*).
Trichomanes parvifolium (Baker) Copel. - gap from Myanmar to W.C. Nepal (Gorkha).
Trichomanes saxifragoides C.Presl - gap from Bhutan to W.C. Nepal (Pokhara).

It is to be hoped that future work, concentrating on Nepal, may continue to make the full distribution patterns of Himalayan pteridophytes clear and other new records may be discovered.

Plate 3: Single frond (abaxial surface) showing the arrangement of the sori.

ACKNOWLEDGEMENTS

The author wishes to thank Mr. C.R. Fraser-Jenkins, of Naya Bazaar, Kathmandu, Research Associate of the Royal Botanic Garden Edinburgh, for helping in identification of the collection, revision of this paper and providing information on disjunct species.

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SHORT NOTE

CORRECTION TO *A REVISED HANDBOOK TO THE FLORA OF CEYLON, VOLUME XV, PARTS A & B, FERNS AND FERN-ALLIES*, 2006. M.D. Dassanayake (General Editor), Monika Shaffer-Fehre (Editor). ISBN, SET 1-57808-411-3

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These volumes devoted to ferns and fern allies contribute to the *Flora of Ceylon*. Unfortunately some errors have been identified.

The following corrections are required to the contents: the family Dryopteridaceae (Vol. A) is treated in two chapters rather than one only, and Polypodiaceae begins Volume B. Regarding the Woodsiaceae, the name of the senior author is missing in 'Contents'; three of the four genera treated, viz.: *Hypodematium, Deparia* and *Athyrium* have been described by C.R. Fraser-Jenkins and one, *Diplazium*, has been contributed by Dr M. Zink. There is one further omission: Vol. B, page 356: PTERIDACEAE, B. Verdcourt. The following text is missing from *Hemionitis tomentosa* at the very end of the treatment:

Specimens Examined. KANDY DISTRICT: Above Kandy: Roseneath Valley, The Heremitage, Sledge 1139 (BM, K); Abatage on Gampola-Pusselawa road, Faden & Faden 76/246 (K); Peradeniya, Matthews s.n.; cultivated at Kew from Ceylon material in 1954 (K).

The editor apologises for these mishaps, and a correct list of contents is given on the next page. The editor would appreciate hearing from readers of any other mistakes. A list of additional corrections will then be published at a later date.

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ACKNOWLEDGEMENTS
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KEY to the FERNS and FERN-ALLIES of SRI LANKA by *P.J. Edwards* *xxi-xxix*

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SHORT NOTE

TWO NEW SPECIES OF *SELAGINELLA* SUBGENUS *HETEROSTACHYS* (SELAGINELLACEAE) FROM THE GUIANAS - A CORRECTION

In the recent paper by Cremers & Boudrie (2007), the two names are ascribed to Valdespino ex Cremers & Boudrie. However, in referring to the descriptions, Cremers & Boudrie state that "what follows" was extracted verbatim from Valdespino's monograph. As both the names and the descriptions are therefore ascribed to Valdespino, under Art. 46.2 the correct attribution of the names should be:

Selaginella gynostachya Valdespino in Fern Gaz. 18: 42[-46]. 2007
Selaginella karowtipuensis Valdespino in Fern Gaz. 18: 46[-51]. 2007.

I thank Professor John McNeill for advice.

CREMERS, G. & BOUDRIE, M. 2007. Two new species of *Selaginella* sugbenus *Heterostachys* (Selaginellaceae) from the Guianas. Fern Gazette 18(2):41-52.

Mary Gibby

MORPHOTYPE AND CONFLICTING TAXONOMIES IN *PTERIDIUM* (DENNSTAEDTIACEAE: PTERIDOPHYTA)

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Key words: Dennstaedtiaceae, bracken, genetics, morphology, morphotype, polymorphism, *Pteridium*, subspecies, taxonomy.

ABSTRACT

Conflicting taxonomic treatments of the diploid bracken ferns of the Laurasian lineage within *Pteridium* are briefly reviewed. The infraspecific entities recognised in this section of the genus can be separated on morphological, phenological and physiological criteria into two main groups referred to respectively as 'aquilinum' and 'latiusculum' morphotypes. Evidence of gene flow between morphotypes is discussed, including the finding from DNA studies that taxa of the 'aquilinum' and 'latiusculum' morphotypes in each major geographic region are more closely related to the contrasting morphotype from the same region than to the corresponding morphotype from another region. It is proposed here that the 'aquilinum' and 'latiusculum' morphotypes may be regarded as mediated by a simple genetic polymorphism involving alternative pleiotropic alleles at a single major morphogenetic locus comparable to those previously described in *Athyrium* and postulated in *Asplenium* and *Pteridium*, but other possible models are discussed.

It is concluded that *P. aquilinum* is best treated as a single species containing at present 11 subspecies.

INTRODUCTION

A vigorous ongoing polemic continues to cloud taxonomic treatment of the diploid (2n = 104; Wolf *et al.*, 1987,1988) bracken ferns [*Pteridium aquilinum* (L.) Kuhn] comprising a Laurasian lineage within the genus. Thomson and colleagues (Thomson, 2004; Thomson *et al.*, 2005; Thomson *et al.*, 2008; *contra* Thomson, 2000) regard *P. aquilinum* as a grouping of 11 subspecies (Table 1) that in general correspond to varieties within Tryon's (1941) *P. aquilinum* subsp. *aquilinum*. In contrast, certain other contemporary classifications are based on separation of these taxa into two phenotypic groups designated here as the 'aquilinum' and 'latiusculum' morphotypes (Table 1). Page (1997) and coauthors (Page & Mill, 1995; Gureyeva & Page 2005) regard these 'aquilinum' and 'latiusculum' morphotypic groups as multi-species complexes represented in Europe by *P. aquilinum* and by *P. pinetorum* C.N. Page & R.R. Mill respectively, each with several subspecies. Fraser-Jenkins (1997), on the other hand, recognises *P. latiusculum* (Desv.) Hieron. ex R.E.Fr. at species level and accords subspecific rank to *P. latiusculum* subsp. *pinetorum* (C.N. Page & R.R. Mill) Fraser-Jenk. Stace (1997) and Karlsson (2000) group the European 'aquilinum' phenotypes as *P. aquilinum* subsp. *aquilinum* and those of 'latiusculum' as *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén. Shorina & Perestoronina (2000) distinguish the European 'latiusculum' morphotype as *P. aquilinum* var. *pinetorum* (C.N. Page & R.R.

Table 1: Geographic distribution and current subspecific nomenclature of northern hemisphere diploid (2n = 104) bracken taxa indicating 'aquilinum' or 'latiusculum' morphotype, together with Tryon's (1941) varietal names for reference.

Geographic region/ morphotype	*P. aquilinum* subspecies	*P. aquilinum* variety
Europe		
'aquilinum'	*aquilinum*	*aquilinum*
'latiusculum'	*pinetorum* (C.N. Page & R.R. Mill) J.A. Thomson[1,2]	*latiusculum* (Desv.) Underw. ex Heller
Asia		
'aquilinum'	*wightianum* (Wall. ex J. Agardh) Shieh[3]	*wightianum* (J. Agardh) R. Tryon
'latiusculum'	*japonicum* (Nakai) A. Löve & D. Löve[1]	*latiusculum* (Desv.) Underw. ex Heller
Africa		
'aquilinum'	*capense* (Thunb.) C. Chr.[4]	*aquilinum*
'latiusculum'	*centrali-africanum* Hieron. ex R.E. Fr.[4]	*africanum* Bonap.
North America		
'latiusculum'	*feei* (W. Schaffn. ex Fée) J.A. Thomson, Mickel & K. Mehltreter[5]	*feei* (W.Schaffn. ex Fée) Maxon ex Yuncker
	latiusculum (Desv.) Hultén auct. Thomson (2004)[1]	*latiusculum* (Desv.) Underw. ex Heller
	pseudocaudatum (Clute) Hultén[5]	*pseudocaudatum* (Clute) Heller
	pubescens (Underw.) J.A. Thomson, Mickel& K. Mehltreter[5]	*pubescens* Underw.
Hawaiian Islands		
'intermediate'	*decompositum* (Gaudich.) Lamoureux ex J.A. Thomson[1]	*decompositum* (Gaudich.) R. Tryon

[1] Thomson, 2004

[2] Also referred to as *P. aquilinum* subsp. *latiusculum* (Desv.) Hultén; *P. aquilinum* var. *pinetorum* (C.N. Page & R.R. Mill) Perestor.; *P. pinetorum* C.N. Page & R.R. Mill; *P. latiusculum* subsp. *pinetorum* (C.N. Page & R.R. Mill) Fraser-Jenk.

[3] Also referred to as *P. revolutum* (Blume) Nakai

[4] Thomson *et al.*, 2005

[5] Thomson *et al.*, 2008

Mill) Perestor.

A dearth of useful discriminatory characters often leads to difficulties in pteridophyte taxonomy, especially in the case of low order taxa that may be separated on as few as one single character (Perrie & Brownsey, 2005). In many fern species the segmental units represented at successive levels by frond, pinna, pinnule, and even pinnulet, form a repetitive hierarchical series for which a feature expressed at one level may not be independent of a corresponding feature scored at another segmental level. In general, such attributes should be treated as relating to a single character, and may well share a common genetic basis. Examples are evident in the morphometric documentation of the relative number, size, shape and spacing of pinnae, pinnules and pinnulets in subspecies of *Pteridium aquilinum* (L.) Kuhn (Thomson *et. al.*, 2005; Thomson *et. al.*, 2008). Further, many commonly used features of indumentum, false indusium and laminal segmentation are extremely labile, being affected by age, shading, water-logging and other environmental conditions (Ashcroft & Sheffield, 1999; Karlsson, 2000; Thomson *et al.*, 2005; Thomson *et al.*, 2008) and must be employed quantitatively and with caution.

Three recent re-evaluations of disputed taxonomic treatments in ferns highlight the contribution that genetic evidence, either directly from breeding experiments or indirectly from molecular data, may make to more consistent and objective assignment of taxonomic rank. In *Athyrium distentifolium* Tausch ex Opiz (Woodsiaceae), morphotype 'flexile' is endemic to Scotland and is found only at localities where 'distentifolium' is also present (McHaffie *et al.*, 2001). Sporophytes of the 'flexile' phenotype are distinguished from 'distentifolium' by frond morphology, position of sori and response to nutrients. The two phenotypes are controlled by alleles of a single major gene with pleiotropic effects expressed in both gametophyte and sporophyte, the 'flexile' morphotype being recessive to 'distentifolium'. In one natural population the frequency of the recessive allele was about 0.4. The two morphotypes were originally described as separate species but McHaffie and colleagues recommend a taxonomic status not higher than variety.

In *Asplenium hookerianum* Colenso (Aspleniaceae), morphotype 'hookerianum' occurs in Australia and New Zealand and is distinguished from the endemic New Zealand morphotype 'colensoi' which has consistently narrower pinnules. Stands in New Zealand commonly comprise morphotype 'hookerianum' alone or co-occurring with 'colensoi': 'colensoi' by itself is rare (Perrie & Brownsey, 2005). The two forms were originally described as separate species. Neither nuclear genomic fingerprinting by AFLP nor the chloroplast sequence results separated the specimens according to morphotype. Geographic source accounts for much more of the total DNA-sequence variation than pinnule morphology in both the AFLP data (29% of genetic variation *versus* 0%) and the chloroplast haplotype data (58% of genetic variation *versus* 3%; Perrie & Brownsey, 2005). Plants of contrasting morphotype originating from close sites are more similar to each other genetically than to plants of the their own morphotype from distant sites. The phenotypic stability of plants of the two morphotypes even when growing intertwined in the field argues against a major role for environmental variables, and 'colensoi' is purported to breed true from spores (Perrie & Brownsey, 2005). It appears probable that morphotypic variation in *Asplenium*, like that in *Athyrium*, results from a simple genetic polymorphism based on allelic variation at a single locus. Perrie & Brownsey (2005) conclude that there is no significant genetic discontinuity between the two morphotypes, and no justification for separating them at

higher than varietal or form rank.

Within *P. aquilinum* in North America, the status of the two eastern taxa now designated subsp. *latiusculum* and subsp. *pseudocaudatum* (Table 1) proved contentious until detailed analyses of morphology and isozyme complements were made by Speer & Hilu (1999) and Speer *et al.* (1999). These taxa are clearly distinct on morphological and distributional grounds (Speer & Hilu, 1999; Thomson *et al.*, 2008). Over their main east-coast range, 'latiusculum' is more abundant in the northern states, 'pseudocaudatum' in the south (Speer & Hilu, 1999), with only very few narrow zones of overlap where intermediates suggesting introgression are seen. Detailed isozyme analyses showed unrestricted gene flow between the two morphotypes at one such zone of co-occurrence (Speer *et al.*, 1999). Speer and colleagues postulate that the 'latiusculum' and 'pseudocaudatum' phenotypes may be controlled by alternative alleles at a single genetic locus with pleiotropic effects. If the 'latiusculum' phenotype is dominant and determined by an allele with high frequency in the north of its range, while the recessive allele for the 'pseudocaudatum' phenotype is at high frequency or fixed in the south, the roughly equal frequencies of the two forms observed in the North Carolina piedmont would correspond to a frequency of about 0.7 for the recessive allele (Speer *et al.*, 1999). Strong selective pressure in relation to environmental features and habitat preference are indicated, with a taxonomic ranking of subspecies for the two morphotypes (Thomson *et al.*, 2008).

CHARACTERISATION OF GENERALISED 'AQUILINUM' AND 'LATIUSCULUM' MORPHOTYPES IN *PTERIDIUM*

Characters that reflect the relative number, relative size, spacing and shape of laminal segments at blade, pinna, pinnule and pinnulet levels (Thomson, 2000; Thomson *et al.*, 2005; Thomson *et al.*, 2008), are particularly effective in discriminating a 'latiusculum'-like group of taxa from an 'aquilinum'-like phenotypic group.

The 'aquilinum' morphotype: Blade long, ovate to linear, typically 2-3 times the length of the longest pinna which is generally one of the third to the fifth pair from the lamina base towards the tip. Pinnae, pinnules (and less markedly pinnulets), relatively long and narrow; typically 13-18 pinnules in the basal half of the longest pinna. Pinnae and pinnules commonly inserted on rachis and costa at 70-90^{o}. Frond expansion gradual, progressing from base to apex. Basal 1-2 pinna pairs often marcescent before expansion of the distal pinnae is complete. Frond axes relatively thick and fibrous; dense stands leave heavy, often partially upright, litter in winter that is slow to collapse next season.

The 'latiusculum' morphotype: Blade short, broadly triangular, typically 1-1.5 times the length of the longest pinna which is generally one of the first or second pair from the base towards the tip. Pinnae, pinnules (and less markedly, pinnulets) relatively short and broad; typically 6-9 pinnules in the basal half of the longest pinna. Basal segment(s) of each order sometimes much reduced, even vestigial. Pinnae and pinnules commonly inserted on rachis and costa at 45-70^{o}. Frond expansion rapid, often almost synchronous, although progressive from base to apex. Basal pinna pairs not marcescent before frond expansion is complete. Frond axes relatively thin, not heavily fibrous; dense stands leave thin litter in winter that collapses readily next season.

The ovate to linear form of the expanded blade and pinna in 'aquilinum' morphotypes results from both the shorter length of the lowest pinna and pinnule pair(s) compared with those placed more centrally and the relatively higher number of these

segments on the frond axis and costa respectively. The broadly triangular frond blade and pinna of the 'latiusculum' morphotype could be envisaged as derived from the 'aquilinum' type by loss of pinna and pinnule pairs from the base of blade and pinna upwards, a process which would at the same time increase the apparent length, relative to more distal segments, of the pinnae/pinnules which thus become the basal or near basal components. Overall the 'latiusculum' morphotype appears to reflect adaptation to conditions providing a short growing season.

Where zones of contact or parapatry occur locally, as in Europe (Rumsey *et al.*, 1991; Karlsson, 2000), NE Asia (Tryon, 1941), and Africa (Verdcourt, 2000), recurrent field observations of morphological intermediates provide evidence of recent, probably ongoing, interbreeding between 'aquilinum' and 'latiusculum' morphotypes. Multi-locus isozyme marker studies also reveal gene flow between multiple genets (Bridges *et al.*, 1998) of subsp. *pinetorum* in Scotland and local populations of subsp. *aquilinum* (Rumsey *et al.*, 1991).

DNA fingerprinting using the Arbitrarily Primed Polymerase Chain Reaction (AP-PCR) and Inter Simple Sequence Repeat (ISSR) procedures show that genomic similarity is higher between 'aquilinum' and 'latiusculum' morphotypes from the same geographic region than either is with morphotypes of its own group from other regions (Thomson *et al.*, 2005; Thomson *et al.*, 2008). Thus subspp. *capense* and *centrali-africanum* from sub-Saharan Africa are more similar genomically than *capense* is to *aquilinum* of Europe or *centrali-africanum* is to the N American *latiusculum* (Thomson *et al.*, 2005; Thomson *et al.*, 2008). Similarly, subspp. *pinetorum* and *aquilinum* of Europe share more genomic markers than *pinetorum* shares with *latiusculum* of North America (Thomson, 2000; Thomson *et al.*, 2005). Chloroplast genome haplotype for the *rps4-trnS* region based on presence or absence of one or both of two 5-base direct repeats is not concordant with the 'aquilinum' or 'latiusculum morphotypic groupings (Thomson *et al.*, 2005; Thomson *et al.*, 2008). For example, the haplotypes (Type A or B, Thomson *et al.*, 2005) of three geographically contiguous 'latiusculum' and 'aquilinum' morphotype pairs are: subspp. *pinetorum/aquilinum* (Europe) respectively Types A and B, subspp. *centrali-africanum/capense* (Africa) both Type B, and subspp. *japonicum/wightianum* (NE Asia) both Type A.

These findings provide strong evidence against a taxonomy based on separation of 'latiusculum' and 'aquilinum' clades (Thomson *et al.*, 2008), and in particular argue against recognition of 'latiusculum' or 'aquilinum' as reproductively-separated groupings that individually merit full species status. Within *Pteridium aquilinum* as recognised here (Table 1), reticulate phylogenetic relationships overlie evolutionary trends presumably based on diversification and local adaptation.

IS THE 'AQUILINUM' VERSUS 'LATIUSCULUM' DISTINCTION A SIMPLE GENETIC POLYMORPHISM?

Descriptively, the morphological polymorphisms analysed in *Athyrium* (McHaffie *et al.*, 2001) and postulated in both *Asplenium* (Perrie & Brownsey, 2005) and *Pteridium* (Speer *et al.*, 1999) behave as if based on variant alleles of major genes, with allele frequencies being maintained by balancing selection pressures in particular environments and/or differentially in the gametophyte or sporophyte stage. The contention that the 'aquilinum' *versus* 'latiusculum' contrast also represents a genetic polymorphism is supported by distributional data (Table 1), the genetic relationships of the contrasting morphotypes in areas of overlap, and evidence that laminal segment

morphology at frond, pinna, pinnule and even pinnulet levels is hierarchically repetitive and likely to be under control of a common gene or genes with alternative, apparently pleiotropic, alleles. Definitive characterisation of the genetic basis of morphotype in bracken must await integrated breeding and molecular analyses. The loci involved are, however, clearly distinct from those responsible for the small-scale morphological variants often collected and cultivated by growers (see, for example, Andersson, 1927) that are rare in natural populations, with very low allele frequencies maintained by recurrent mutation opposing negative selection (McHaffie *et al.*, 2001).

While for descriptive purposes morphotypic variation in the ferns discussed here may be adequately treated in terms of single locus polymorphisms with pleiotropy, functional and structural molecular analyses of the loci responsible are now required to reveal how the underlying developmental process are controlled. In general, the more numerous and diverse the multiple phenotypic effects involving disparate morphological and physiological characteristics that appear to be under single gene control, the more an explanation invoking pleiotropy becomes questionable. In the present cases we therefore need to consider other possible models of gene structure such as that exemplified by the complex S locus responsible for self-incompatibility (SI)/compatibility (SC) in a number of families of flowering plants such as Brassicaceae. This super-locus provides co-ordinated unitary genetic control over multiple aspects of SI mediated by tightly linked co-adapted sequence segments collectively forming an S haplotype (Charlesworth *et al.*, 2005). Multiple developmental, cellular, physiological and biochemical processes in different S phenotypes are mediated by the alternative S haplotypes represented in polymorphic populations or in different taxa (Bechsgaard *et al.*, 2006; Sherman-Broyles *et al.*, 2007). The several features characterising each S phenotype are controlled by distinct sequence elements and do not involve pleiotropy. Where aspects of phenotype are controlled by a complex super-locus or through a stepwise multigene pathway, multiple mutations may appear as a single event if a mutation acting at an early step blocks expression of accumulated changes effective later in the pathway. If features distinguishing allopatric morphotypes are subject to selection, the allelic variants responsible will be expected to change in frequency more rapidly than 'neutral' genomic elements. Phenotypic features under positive selection are likely to become fixed faster than other genomic segments so that the probability of finding DNA sequence markers correlating with morphotype is expected to be low, increasing with the time of separation of the contrasting forms. In *Asplenium*, Perrie & Brownsey (2005) found that neither AFLP fingerprinting of the nuclear genome nor chloroplast sequence data grouped the plants analysed according to their morphotype. In *Pteridium*, Thomson (2000) identified markers detected by AP-PCR that are specific to subsp. *wightianum* (as *P. revolutum*) and other markers that are specific to subsp. *capense* [misnamed by Thomson (2000) as *P. aquilinum* var, *africanum*; see Thomson *et al.*, 2005). These major markers are in both cases restricted in occurrence to geographically localised taxa here regarded as of subspecific status, and neither is shared by other 'aquilinum' morphotypes. Distinctive alleles, supergene haplotypes and/or modified dominance relations may account for the 'intermediate' morphotype of subsp *decompositum* (Table 1) in which genomic elements of both subsp. *japonicum* ('latiusculum') and subsp. *wightianum* ('aquilinum') are present (Thomson, 2000).

CONCLUSIONS

In most taxonomic investigations of ferns, especially where multiple taxa must be considered, controlled breeding experiments of the kind so admirably applied in *Athyrium* (McHaffie *et al*., 2001) are not practicable. More widely feasible are genomic comparisons based on methodologies such as AP-PCR (RAPD), AFLP, ISSR, or microsatellite analyses. If plants of taxon A from locality 1 are more closely related genetically to plants of taxon B from locality 1 than to taxon A plants from localities 2...n, and/or a comparable situation holds for the relationships of taxon B, there is *prima facie* evidence of recent and/or ongoing gene flow between the taxa that is likely to be inconsistent with the degree of reproductive isolation normally associated with full specific status. Rather, such a situation strongly suggests that the taxa concerned should be accorded infraspecific rank, for example as subspecies, varieties, or forms (Perrie & Brownsey, 2005; Thomson *et al*., 2008).

The work of McHaffie and colleagues on the 'distentifolium'/'flexile' polymorphism in *Athyrium* represents an extraordinary contribution to our understanding of fern morphogenetics by showing how morphological and physiological studies of the gametophyte as well as the sporophyte may reveal at these two life stages 'antagonistic pleiotropy' (Shaw, 2001) that determines allele frequencies in natural populations through otherwise unsuspected opposing positive and negative selective pressures. However, as pointed out above, questions remain open regarding the structure of the genetic loci involved in the control of fern morphotype, and thus on the strict applicability of the term pleiotropy in these cases.

P. aquilinum appears at present to be best treated as a single species containing 11 subspecies as listed in Table 1. Further morphometric and genetic studies are needed to clarify the status of a number of named taxa described from many parts of Eurasia which on present evidence should, if named, be ascribed varietal, form or ecotype rankings (Stace, 1997).

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BOOK REVIEW

THE LIVERWORTS, MOSSES AND FERNS OF EUROPE, BY WOLFGANG FREY (HORNWORTS AND LIVERWORTS), JAN-PETER FRAHM (MOSSES), EBERHARD FISCHER AND WOLFRAM LOBIN (FERNS AND FERN-ALLIES). Translated and updated by the authors with illustrations prepared by H. Lunser (Bryophytes) and E. Fischer (Ferns). Harley Books. English edition revised and edited by T.L.Blockeel .2006. 512pp.(ferns and former fern allies pp.363-455), 166 figs, each incorporating numerous line drawings (ferns and former fern allies figs. 121-166). 218 X 155mm, hardback. ISBN 0 946589 70 4. £45. German edition first published 1995.

Wide ranging titles such as this usually mean a book will be a 'Jack of all subjects' and master of none, so you can imagine the pleasant surprise I had on dipping into it. Ferns are indeed a relatively minor part filling fewer than 100 pages but the coverage is more comprehensive than given in many field handbooks.

Apart from a couple of prefaces there are no introductory chapters. The books start straight away with the dichotomous keys. At the end there is a glossary and bibliography.

None but the most well read specialist will be familiar with all the taxa described here. Recently discovered species and subspecies are included. There are no lengthy field notes, details are precise and to the point. Most species are covered with fewer than four lines of text. Distribution is given by country or island within Europe and more briefly outside of Europe. As with the rest of the book the entire fern section is a generously annotated dichotomous key. The key is supported by many line drawings which work well for the well defined species but by the time you get down to the really critical taxa they are not so helpful. I looked long and hard at one sketch of the base of the lowermost pinna of *Gymnocarpium robertianum* but I still cannot work it out!

The fern tourist venturing anywhere in Europe, be it the Azores, Crete, Cape Verde, Madiera, Russia or closer to home will find all the local fern species covered. A few hybrids are also mentioned although the criteria for their inclusion is obscure to me. For example the very rare *Aspelnium x heufleri* is in the key but many others, such as *A. x sarniense*, are not.

I can think of no other up to date book covering all the ferns of Europe. Remy Prelli`s *Les fougeres et plantes allies de France et d'Europe occidentale* has a more restricted range. Where the two overlap I suggest the Prelli book will be the more user friendly even though it is in French. For full coverage of Europe in one go, however, this guide is a useful volume.

Martin Rickard

BOOK REVIEW

BIOLOGY AND EVOLUTION OF FERNS AND LYCOPHYTES. Tom A. Ranker & Christopher H. Haufler (eds). 2008. 480pp., 66 line figures 45 halftones. ISBN 978-0521-87411-3 hardback; ISBN 978-0521-69689-0 paperback. Cambridge University Press. £75.00, £35.00.

The editors of this new book have taken up the challenge of presenting the reader with the major research developments that have taken place over the last 10 years that contribute to the current understanding of the biology of ferns and lycophytes. To achieve this goal they have brought together the work of some 28 contributors all active in research, mainly from USA but also from Canada, Europe and Japan.

The subject areas are diverse. The first section on development and morphogenesis starts with the gametophyte and alternation of generations, before exploring the structure of meristems and subsequent diversification into the various organs – root, stems and leaves. The next section deals with genetics and reproduction, including chapters on the role of antheridogens, breeding systems, and the chloroplast and nuclear genomes. Ecology is a complex discipline in itself, and the focus here is on phenology and habitat specificity in tropical ferns, the ecology of gametophytes and a review of conservation biology. The final section, systematics and evolutionary biology, includes a review of the evolution of ferns and fern-like plants from the fossil record, a chapter on species and speciation, exploration of diversity, biogeography and floristics, and ending with phylogeny and classification.

Each chapter presents a personal review of the subject by it author(s), with summaries of discoveries and developments, explanations of concepts and ending with a section on prospects for the future - all supported by an extensive list of references.

This is a scholarly work, clearly aimed at the undergraduate student market, and I can see it being added to the essential reading list for many courses in plant evolutionary biology. But it is more than being a standard undergraduate textbook and with such a wide variety of topics covered, there will be sections to interest a variety of general readers and particularly for those with a fascination for fern biology. It is good to see that it available as a more modestly priced paperback as well in hardback format.

Mary Gibby

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